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SYSTEMATICS AND BIOGEOGRAPHY OF NORTH PACIFIC SHAGS, WITH A DESCRIPTION OF A NEW SPECIES

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The most derived clade of shags (Phalacrocoracidae: Leucocarboninae) are the Cliff Shags (*Stictocarbo* spp.), a diverse assemblage of slender-bodied marine birds restricted to neritic waters and coastlines. Cliff Shags are found in New Zealand waters, Europe, the west coast of the Americas, and the north rim of the Pacific Ocean (Siegel-Causey, 1988; Siegel-Causey and Litvinenko, 1992). Two species are known from North America: Pelagic and Red-faced Shags (*Stictocarbo pelagicus* and *S. urile*). These birds are widely distributed in the North Pacific basin and are sympatric throughout Beringia and the North Pacific, including the Aleutian and Kurile Islands, the Soviet Far East, and Sea of Japan.

Recent archaeological excavation of Aleut kitchen middens on Amchitka Island in the far western part of the Aleutian Islands provided an opportunity to examine the population history of Aleutian shags. My study of this material (Siegel-Causey and Lefevre, 1991) revealed a diverse fauna of cormorants and shags, some of which are not resident on Amchitka Island at present.

Throughout all strata and sites of these middens, I found in total 109 elements of a small phalacrocoracid that were not referable to any known species. The majority were bones of the limbs and central core, although there were a few cranial and mandibular fragments, furculae, and a sternum. I found diagnostic qualitative characters on the mandible, furcula, humerus,

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carpometacarpus, synsacrum, femur, tibiotarsus, and tarsometatarsus that served to refer these elements to the genus *Stictocarbo* and to discriminate them from Pelagic and Red-faced Shag bones (Appendix 1). Furthermore, all of these bones were mensurally smaller than any of the extant species on Amchitka Island (Table 1), and could be sorted easily from the other midden elements by size alone.

Size is unreliable as a character, however, when the scope of comparison broadens beyond a single locality. Pelagic Shags, for example, demonstrate substantial clinal variation in size over their distribution (Siegel-Causey, in prep.) and some specimens collected from the southern limits of the range approach the size of these enigmatic midden bones. For these and other reasons, I will employ robust analyses of the qualitative and quantitative patterns of morphometric variation in these North Pacific shags rather than rely on more simplistic univariate and descriptive accounts.

The discovery of a previously unknown shag on Amchitka Island prompted me to search among all existing museum specimens from Beringia for evidence of more recent presence in this region. Because external characters are unknown and the only specimens are skeletons, it was not possible to identify museum skins of this species. I found three skeletal specimens, all collected coincidentally from Amchitka Island in the late 1950s, possessing all of the qualitative characters identified from midden bones and within the expected size range. This wealth of data makes possible a more detailed analysis of the phylogenetic status and relationship of this new taxon.

METHODS

Subfossil material and skeletal specimens.—Bird bones were collected from two sites on Amchitka Island by employees of Archaeological Research, Inc. during the summer of 1969 and were later sorted to family by Stuart Warter (see Acknowledgments). All subfossil material is kept at California State University at Long Beach and was made available to me through the auspices of Warter. Full details on the provenance of these bones and other information relating to Amchitka Island are given in Siegel-Causey and Lefevre (1991). I obtained from various sources (see Acknowledgments) comparative skeletal specimens collected at or near breeding colonies in Beringia; a list of specimens and museums is available from the author. Museum specimens are identified by accession number and the following acronyms: AMNH (American Museum of Natural History), CSULB (California State University, Long Beach), KU (Museum of Natural History, University of Kansas), LACM (Los Angeles County Museum of Natural History), UMMZ (Museum of Zoology, University of Michigan), USNM (U.S. National Museum of Natural History), UWBM (Burke Museum, University of Washington), and UWZM (Zoological Museum, University of Wisconsin).

Table 1. Univariate statistics for skeletal characters of North Pacific Shags, genus *Stictocarbo*. Measurement codes appear in parentheses in the character column and refer to Figure 12 in Ono (1980). NA means not available.

Character ^{1,2}	<i>wile</i> (<i>n</i> = 17)	<i>pelagicus</i> (<i>n</i> = 20)	<i>kenyoni</i> (<i>n</i> = 3)	midden bones (<i>n</i> = 109) ³
Cranium				
L ^c (NA)	53.8 (0.5) ⁴	51.8 (0.6)	46.3 (0.9)	NA
GW ^a (NA)	30.8 (0.2)	28.5 (0.2)	26.4 (0.1)	NA
frontonasal W ^c (NA)	12.8 (0.3)	12.6 (0.2)	9.9 (0.7)	NA
postorbital W ^a (NA)	24.5 (0.4)	22.1 (0.4)	20.6 (0.1)	NA
Maxilla				
L ^a (NA)	59.1 (0.5)	56.2 (0.6)	50.9 (0.2)	NA
GW ^c (NA)	11.0 (0.2)	10.8 (0.2)	8.8 (0.2)	NA
D ^c (NA)	5.9 (0.2)	22.1 (0.4)	4.1 (0.1)	NA
Coracoid				
L ^c (Ca)	70.3 (0.9)	65.3 (0.6)	57.7 (0.2)	56.7 (0.3) [10]
sternal W ^c (Cf)	22.3 (0.3)	20.3 (0.3)	17.9 (0.7)	17.2 (0.9)
Humerus				
La (Ha)	134.1 (1.5)	125.7 (1.2)	108.4 (2.5)	111.4 (2.7) [7]
shaft DW ^a (He)	7.9 (0.1)	7.3 (0.1)	6.3 (0.1)	6.7 (0.3)
head W ^a (NA)	24.4 (0.3)	22.5 (0.2)	20.0 (0.2)	20.4 (0.7)
distal W ^c (NA)	15.0 (0.2)	13.6 (0.2)	12.2 (0.4)	12.3 (0.3)
Radius				
L ^c (Rb)	144.4 (1.8)	129.5 (2.8)	114.4 (0.8)	113.3 (0.9) [4]
shaft PW (NA)	5.0 (0.4)	4.5 (0.4)	4.2 (1.5)	4.1 (0.8)
distal W ^b (Re)	8.8 (0.1)	8.4 (0.1)	7.6 (0.1)	7.4 (0.4)
Ulna				
L ^a (Ub)	143.3 (1.7)	133.1 (1.3)	118.9 (0.2)	114.5 (0.3) [7]
shaft PW ^c (Ui)	13.1 (0.2)	11.5 (0.4)	10.2 (0.2)	10.0 (0.2)
distal W ^c (Uh)	10.8 (0.1)	10.4 (0.1)	9.7 (0.1)	9.5 (0.4)
Carpometacarpus				
total L ^b (Ca)	64.1 (0.7)	60.6 (0.6)	54.4 (0.1)	54.6 (1.6) [19]
shaft PW (Cf)	4.7 (0.1)	4.4 (0.1)	4.4 (0.5)	4.1 (0.4)
distal W ^b (Cc)	13.5 (0.1)	12.7 (0.1)	11.5 (0.2)	11.8 (0.4)
Synsacrum				
total L ^b (Pc)	109.5 (1.1)	103.4 (0.9)	90.9 (2.0)	87.9 (2.5) [12]
acetabular D (Pb)	18.6 (0.2)	16.9 (0.4)	16.3 (0.5)	16.2 (0.9)
acetabular W ^b (Ph)	35.3 (0.4)	33.0 (0.5)	29.5 (0.7)	31.2 (1.3)
Femur				
total L ^b (Fa)	61.3 (0.7)	55.5 (0.5)	49.1 (1.0)	49.6 (0.8) [15]
neck GW ^b (Fe)	15.8 (0.3)	14.2 (0.2)	12.2 (0.3)	12.6 (0.4)
shaft DW ^a (Fc)	7.6 (0.1)	7.1 (0.2)	6.7 (0.2)	6.2 (0.4)
distal W ^b (Fh)	15.6 (0.2)	14.4 (0.2)	12.8 (0.1)	12.3 (0.4)

Table 1. Continued.

Character ^{1,2}	<i>wile</i> (<i>n</i> = 17)	<i>pelagicus</i> (<i>n</i> = 20)	<i>kenyoni</i> (<i>n</i> = 3)	midden bones (<i>n</i> = 109) ³
Tibiotarsus				
total L ^b (Tib)	111.6 (1.1)	102.1 (0.9)	91.7 (1.1)	NA
head GW ^c (Tif)	12.4 (0.1)	11.2 (0.1)	10.0 (0.2)	NA
shaft DW ^b (Tid)	6.9 (0.1)	6.6 (0.1)	5.4 (0.1)	NA
distal W ^b (Tii)	12.0 (0.2)	11.1 (0.1)	10.0 (0.3)	NA
Tarsometatarsus				
total L ^b (Tab)	55.6 (0.6)	53.0 (0.5)	47.8 (0.5)	47.4 (0.6) [14]
proximal GW ^b (Tac)	13.0 (0.2)	12.2 (0.1)	10.8 (0.3)	11.2 (0.6)
hypotarsus D (Taf)	15.8 (0.4)	15.3 (0.2)	13.9 (0.2)	13.8 (0.6)
hypotarsus W ^a (Tae)	6.5 (0.1)	5.7 (0.1)	4.7 (0.1)	4.6 (0.4)

¹ D = depth, DW = distal width, GD = greatest depth, GW = greatest width, L = length, LW = least width, PW = proximal width, W = width.

² Superscript letters indicate significance level of species differences in ANOVA: a = $P < 0.05$, b = $P < 0.001$, c = $P < 0.001$.

³ Elements are unassociated. Sample sizes are given separately in brackets.

⁴ Mean (SEM).

Phylogenetic analysis.—Each of the qualitative osteological characters used was a discrete trait in which I could obtain at least two discrete states. I found several other characters having modal states in some specimens; however, because the source of character variation in phalacrocoracids is little known, I excluded these from the initial analysis. (See below for further discussion on character variation.) I added them subsequently to the reduced set and tested for stability of the resultant tree(s). If tree topology was unchanged from the initial analysis, I used the character; if otherwise, I excluded the character. In other words, I in effect mapped the variable characters on the tree derived from the reduced data set and calculated summary tree statistics from the augmented data set.

I determined polarities of each character using methods described in Siegel-Causey (1988). Transformation series described as characters 13 and 14 were treated as unordered. The trees were described using PAUP 3.0G (Swofford, 1990) and I used the Exhaustive Search method which guarantees finding all possible trees. There were no differences in character placement using the accelerated transformation (ACCTRAN) or delayed transformation (DELTRAN) optimizations. Complete details on terminology, methodology, and rationale of phylogenetic systematics are given in Wiley, et al. (1991). See Appendix 1 for character descriptions and polarities and Appendix 2 for the data matrix of character state codings for North Pacific shags.

Statistical analysis.—For mensural comparisons among taxa, I used only specimens which had a full component of study elements; thus, I used partial skeletons that had at least one of each element listed in Table 1, but I excluded all specimens with elements missing from this list. I did not measure sterna because, for the sample of skeletons I was able to measure, more than half had damaged or warped sterna.

The only exception to this policy involved use of the midden material in univariate comparisons with the putative specimens of the new taxon. Summary statistics of these measures are reported in Table 1, but no midden bones were used in subsequent multivariate analyses.

Skeletal measures used in this study are a subset of those detailed in Ono (1980); Table 1 references Ono's measurements where appropriate. Because of the small number of specimens and the high number of unsexed specimens, I pooled sexes even though cormorants and shags show great sexual dimorphism. In all, I used 40 specimens for multivariate comparisons (*S. urile*: 10 males, 7 females; *S. pelagicus*: 4 males, 8 females, 8 unsexed; *S. new species*: 1 female, 2 unsexed).

I analyzed interspecific differences in skeletal measures using a stepwise multivariate analysis of variance and ANOVAs of scores derived from stepwise Canonical Analysis (CA) which were used to quantify maximum interspecific differences. All of the multivariate techniques were performed on log-transformed measurements. Statistical analyses were done using computer programs available in BMDP (Dixon, 1988).

RESULTS

Description of new species.—The abundance of subfossil elements and three extant skeletal specimens makes possible a description of this new taxon of North Pacific shags.

Stictocarbo kenyoni, new species

Fig. 1

Holotype.—USNM 431164, complete skeleton from an adult female from Constantine Harbor, Amchitka Island, Alaska; collected 22 February 1959 by Karl W. Kenyon from a fish net. Mass of the specimen at the time of collection was 2 lb 6 oz (1060 g).

Paratypes.—UWBM 18613 and 18614 (unsexed birds originally identified as *Phalacrocorax pelagicus*, Constantine Harbor, Amchitka Island, Alaska, collected 15 September 1957 by K. W. Kenyon). Subfossil skeletal material (CSULB 14011–14119) from Amchitka middens 31 and 36 is referred to this species.

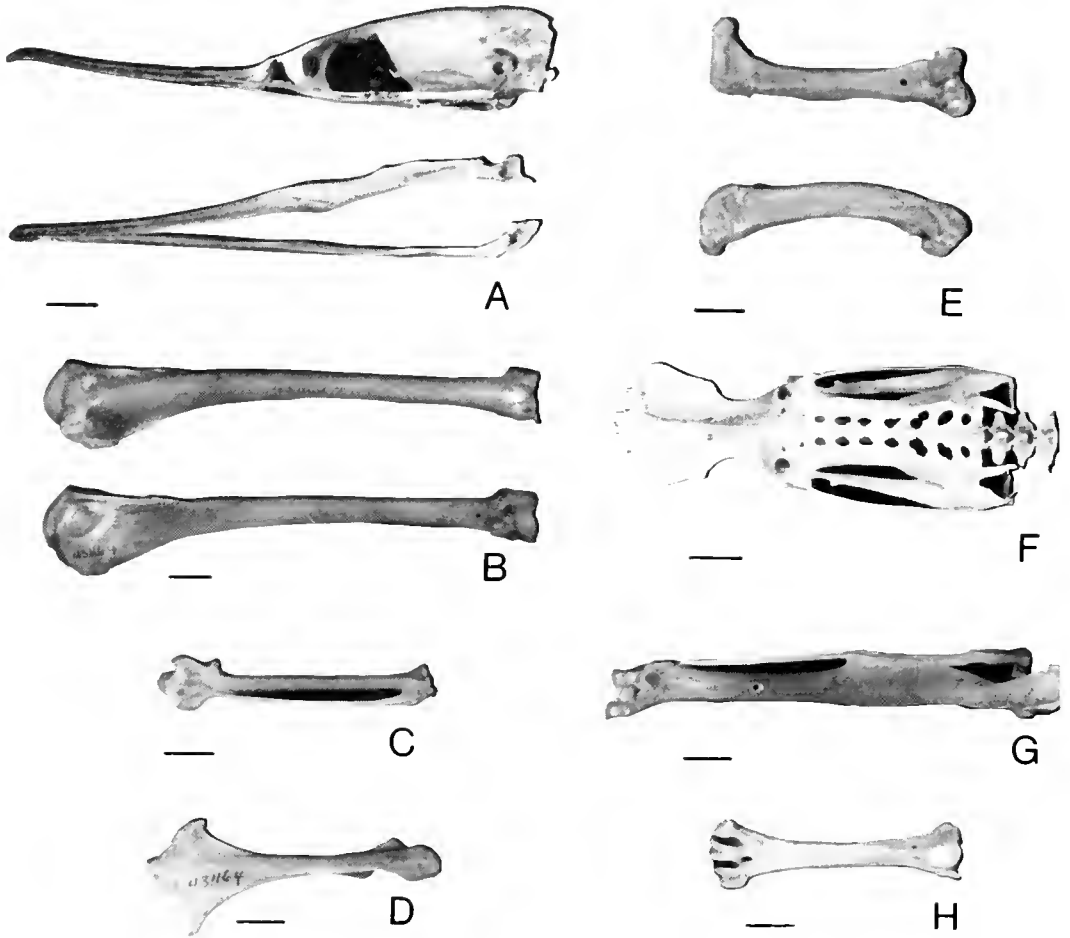


Fig. 1. Type of *Stictocarbo kenyoni*, new species (USNM 431164). A. Skull and mandible, left side. B. Humerus: top, anconal left side; bottom, palmar right side. C. Carpometacarpus, anterior, left side. D. Coracoid, anterior, left side. E. Femur: top, posterior left side; bottom, lateral right side. F. Synsacrum, posterior view. G. Tibiotarsus, anterior left side. H. Tarsometatarsus, posterior right side.

Diagnosis.—*Stictocarbo kenyoni* is similar to *S. urile* but may be distinguished from it and *S. pelagicus* by its small size and by six autapomorphic skeletal characters (Appendix 1). The fossa aditus of the mandible extends at least $\frac{3}{4}$ of the length of the insertion of *M. pseudotemporalis* (character 1). The attachment of *M. dorsalis scapulae* on the humerus is present as paired scars in line on the bicipital crest (char. 5). The attachment of *M. obturator externus* + *internus* on the femur is deeply excavated and narrow (char. 13). The attachment of *M. flexor perforatus digiti II* on the femur is deeply excavated with a robust lateral bony crest (char. 14). The medial margin of the attachment of *M. flexor hallucis longis* on the femur is coincident with the medial prominence of the lateral condyle, causing its superior aspect to appear sharply produced (char. 16). The supratendinal bridge of the tibiotarsus has distinctly linear, parallel margins (char. 19).

Description.—The holotype shares two synapomorphic characters with its congeners *S. pelagicus* and *S. urile*. On the femur, the attachment of *M.*

flexor perforatus digiti III lies on the medial edge of the bone (char. 15), and on the tarsometarsus the medioplantar process of trochlea metatarsus II is produced proximally (char. 24). It shares with *S. urile* seven unique skeletal characters: (a) the anterior attachment of *M. pectoralis superficialis* pars superficialis is parallel with the anterior edge of the furcula (char. 3); (b) the ligamental furrow on the humerus is marked by a deep fossa on the medialmost part (char. 6); (c) the infratrochlear fossa of the carpometacarpus is indistinct (char. 9); (d) the area immediately adjacent to the supratrochlear fossa of the carpometacarpus is unexcavated (char. 10); (e) the attachment of *M. obturator externis* on the synsacrum is unexcavated (char. 11); (f) the intercotylar fossa of the tarsometatarsus is absent or convex (char. 22); and (g) only digit III has a deeply excavated supratrochanteric dorsal fossa (char. 23). In addition, it differs from *S. pelagicus* in that the attachment of *M. adductus mandibulae externus superficialis* on the mandible is indistinct rather than expressed as a strong transverse ridge (char. 2), and also that the lateral edge of the humeral pneumatic fossa is planar in the holotype rather than marked by a distinct narrow excavation (char. 4).

External features.—External phenotypic features are unknown, except for Kenyon's (pers. comm.) impression that the bills of the types were very thin which is reflected by the significantly narrow width of the maxilla found in the types (Table 1). I found several museum skin specimens originally identified as Pelagic Shags that approached the small size of the type skeletons. Because size is unreliable for identification in this clade (see below), identification of these skins must remain problematic unless skeletal elements contained within them provide positive means of identification. Until additional specimens are collected or identified, the external appearance of this species remains a mystery.

Description of paratypes.—Paratypes differ from the holotype only in minor details related to size; skeletal material from the referred midden material shows evidence of wear and aging.

Measurements.—See Table 1.

Distribution.—Known only from Amchitka Island, Alaska.

Etymology.—This species is named after Karl W. Kenyon, who collected all known extant specimens of this new shag, and whose pioneering work on the Aleutian avifauna greatly advanced our understanding of the ecology of North Pacific seabirds.

Common name.—Kenyon's Shag.

Skeletal specimens examined.—*Stictocarbo urile*. USA: Amak Islands (USNM, UMMZ, UWZM, 8 ♂, 2 ♀), St. Matthew Island (USNM, 1 ♂), Pribilof Islands (KUMNH, USNM, UMMZ, UWZM, 6 ♂, 4 ♀), Southeast Alaska (USNM, 5 ♂, 3 ♀), Cape Thomson (KUMNH, 1 ♂); USSR: Kommandarski Islands (USNM, 1 ♂); JAPAN: Hokkaido (USNM, 1 ♂, 1 ♀).

S. pelagicus. USA: West Coast (USNM, CAS, FM, 6 ♂, 4 ♀, 1 ?), Southeast

Alaska (USNM, UWZM, UMMZ, 4 ♂, 3 ♀), Amchitka Island (USNM, UWBM, 5 ♂, 2 ♀, 3 ?), Amak Islands, (USNM, UMMZ, 1 ♂, 1 ♀), Pribilof Islands (KUMNH, 1 ♂, 1 ♀); CANADA: Mandarte Island (1 ♀); USSR: Kommandarski Islands (USNM, 1 ♀), Siberia (USNM, 2 ♂, 1 ♀); JAPAN: (USNM, 1 ♀).

MENSURAL COMPARISONS

Univariate comparisons.—Thirty-three of 37 skeletal measurements differed significantly among species (Table 1); the other four were width or depth measures which lacked significant power in discriminating among taxa. Those measurements effecting the greatest difference among species were length and greatest widths of limb elements and width of trunk elements and cranium. *Stictocarbo kenyoni* had the smallest means for all measures, *S. wile* the largest.

None of the dimensions of the types differs significantly from means obtained from individual midden elements (*t*-tests, $P < 0.05$). I conclude therefore that the type specimen and unassociated midden elements represent the same taxon. Midden elements were excluded from all multivariate analyses.

Canonical analysis.—North Pacific shags were separated completely (Fig. 2) by species using a stepwise canonical analysis of complete skeletons (Wilk's $\lambda = 0.0516$, $df = 19, 1, 40$). Two axes were sufficient to explain all of the variance in canonical space. Prior identifications were by qualitative characters; all pairwise discriminations between species were significant ($P < 0.001$, pairwise *F*-tests, $df = 19, 22$), and jackknifed classifications of specimens to species were 100% correct. Nineteen of the skeletal variables (Table 2) were incorporated significantly into the model (partial *F*-tests, $P < 0.05$). Species differences were significant on both canonical axes (ANOVA on canonical scores, $P < 0.0001$).

Geographic variation.—The sample sizes were inadequate for all taxa to allow a quantitative assessment of geographic variation in skeletons. It is worth noting, however, that specimens collected from the southern limits of the range of Pelagic Shags (Fig. 2, closed circles), while small and close in size to Kenyon's Shag, were classified unambiguously by stepwise DFA as Pelagic Shags. These small southern Pelagic Shags represent a lower bound for multivariate variation in this taxa and none possessed the qualitative characters found in Kenyon's Shag.

QUALITATIVE COMPARISONS

Phylogenetic relationships.—My preliminary observations indicated that this new species is a shag (Leucocarboninae) and a member of the Pelagic–Red-faced Shag clade (genus *Stictocarbo*). Phylogenetic analysis using PAUP

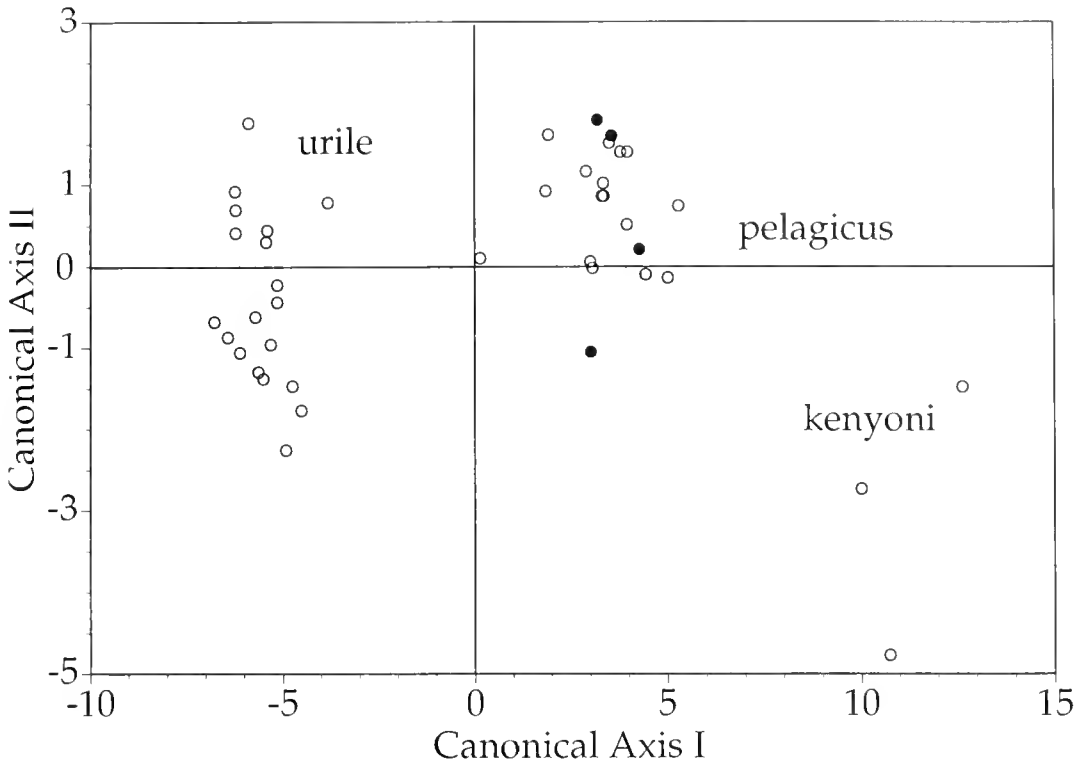


Fig. 2. Plot of scores of North Pacific Shags on canonical axes I and II. Specimens were identified using qualitative osteological characters. The closed circles represent Pelagic Shags collected from central California.

on 24 osteological characters and polarities given in Appendix 1 produced a single tree. This tree (Fig. 3) has a length of 24 steps and $CI = 0.923$, excluding autapomorphies.

Seven autapomorphies support the establishment of this taxon as a new species. One (char. 5) relates to greater control of humeral rotation and possibly more powerful flight (see Owre, 1967). Three (char. 13, 14, 15) relate to extension of the foot and flexion of digits and may represent increased capabilities in underwater propulsion (see Owre, 1967). One (char. 7) is homoplasious and is convergent to states observed elsewhere in the family (e.g., *Nesocarbo campbelli*, *Microcarbo* spp.) (Siegel-Causey, 1988). Functions of the other characters are unknown.

Eight synapomorphies, six of which are unambiguous, establish the Red-faced Shag as sister species to this new taxon. Two of the six (char. 3, 6) relate to greater range in wing movement (see Owre, 1967), but the functions of the remaining characters are obscure. Two (char. 12, 17) are homoplasious with states present elsewhere in the genus and relate to more powerful action of the hind limb (see Owre, 1967; Siegel-Causey, 1988). Two synapomorphies (char. 15, 22) unite all three extant species as a clade; the first reflects a broad degree of digital flexion, but the function of the other is obscure.

Table 2. Standardized canonical coefficients of skeletal variables on canonical axes for North Pacific Shags, genus *Stictocarbo* ($n = 40$).

Character	Standardized coefficient ¹	
	CA I	CA II
Bill GW	1.72	0.51
Coracoid L	4.37	-0.62
Coracoid sternal facet W	0.42	0.43
Humerus L	-2.11	0.66
Humerus DW	-1.09	-0.16
Radius L	2.24	0.10
Radius DW	-0.68	-0.39
Carpometacarpus shaft W	0.88	-0.14
Synsacrum L	1.52	0.67
Synsacrum D	-3.15	-0.66
Synsacrum W	-2.16	-0.64
Femur L	-1.07	-0.38
Femur head W	-1.27	-0.08
Femur shaft DW	-0.68	-0.28
Tibiotarsus shaft DW	-1.30	0.74
Tibiotarsus DW	1.05	0.15
Tarsometatarsus L	-1.61	0.14
Tarsometatarsus PD	0.73	-0.22
Hypotarsus W	-1.72	-0.44
Eigenvalue	29.9	1.08
Percentage of variance	0.96	0.04
Among-species F^2	31.04*	0.21

¹ Standardized by pooled within-group variances.

² Significance levels of F -values ($df = 2, 38$): * $P < 0.001$

Specimen variation and identification.—An important factor associated with skeletal specimens is the degree of confidence that can be given to field identifications. In some cases, particularly in groups where species appear similar or have been little-studied, misidentifications may be prevalent. There seem to have been few mistakes in identification of most specimens of Pelagic and Red-faced Shags collected as adults in breeding plumage. For all other ages and plumages, however, identifications are often problematic and based on typological constructs such as collection location or specimen size. Mistaken identifications frequently occur because juvenile Red-faced and Pelagic Shags are phenotypically similar and small Red-faced females and large Pelagic males in basic plumage are confusing (Siegel-Causey, in prep.). Therefore, it was critical to this study that I examined as many skeletons as

possible that were collected from known breeding localities. The number of specimens encompassing the geographic range of the clade of North Pacific shags is small; in all, I examined only 53 specimens not including the specimens of Kenyon's Shag.

Using qualitative characters, I determined that eight of the skeletons I used were misidentified (not including those subsequently identified to be Kenyon's Shag). Four of these (UMMZ 224301, 224304, 224305, 224310) were originally identified as Red-faced Shags, but closer examination of qualitative characters revealed that they were probably Pelagic Shags, albeit large for their gender. The other four (KU 60506, 60507, UWZM 15960, USNM 431371) were problematic and presented many difficulties in character assignment. I coded these eight as unknowns, and excluded them from the initial analysis. I discuss elsewhere (Siegel-Causey, in prep.) the relevance of these specimens in the context of widespread geographic variation.

For the most part, the remaining 40 specimens presented few problems in identification or in assessment of character states. For all of the Pelagic Shags used in this study, character states did not vary and I was unable to document any variation other than minor differences associated with size or gender. Nine characters, however, varied among the 17 skeletal specimens of Red-faced Shags that I used, and these may indicate imprecise character state definitions, intermediate states of mosaic characters, or natural variation (Appendix 1). Within *S. urile* most of these state variants could be attributed to underdeveloped or indistinct muscle scars or to pathology (e.g., UMMZ 224304 has oddly foreshortened humeri and concomitant change in the bony evidence of muscle attachment). By contrast, two characters (12, 33) had moderate variation among 10 specimens by character states intermediate to those expected for any of the species. Deletion of these characters, however, did not affect the stability of the tree shown in Fig. 3; further study on the nature of character variation is needed before they are discarded from consideration in phylogenetic analyses.

SYSTEMATICS AND BIOGEOGRAPHY

There is an additional member of the clade that includes *S. pelagicus*, *S. urile*, and *S. kenyonii*. Chandler (1990) described a fossil shag from late Miocene (Blancan, 2–3 mybp) sediments near San Diego, California. This species, *Stictocarbo kumeyaay*, is represented by several upper and lower limb elements having sufficient characters to allow him to establish it unambiguously as belonging to the clade of North Pacific shags (see also Appendix 1, Fig. 3). By close examination of these elements and characters, I was able to determine that this fossil shag is primitive to the extant species. Two characters were especially indicative of the derived state of the other three shags. The cnemial crests of the tibiotarsus are spaced less than the width

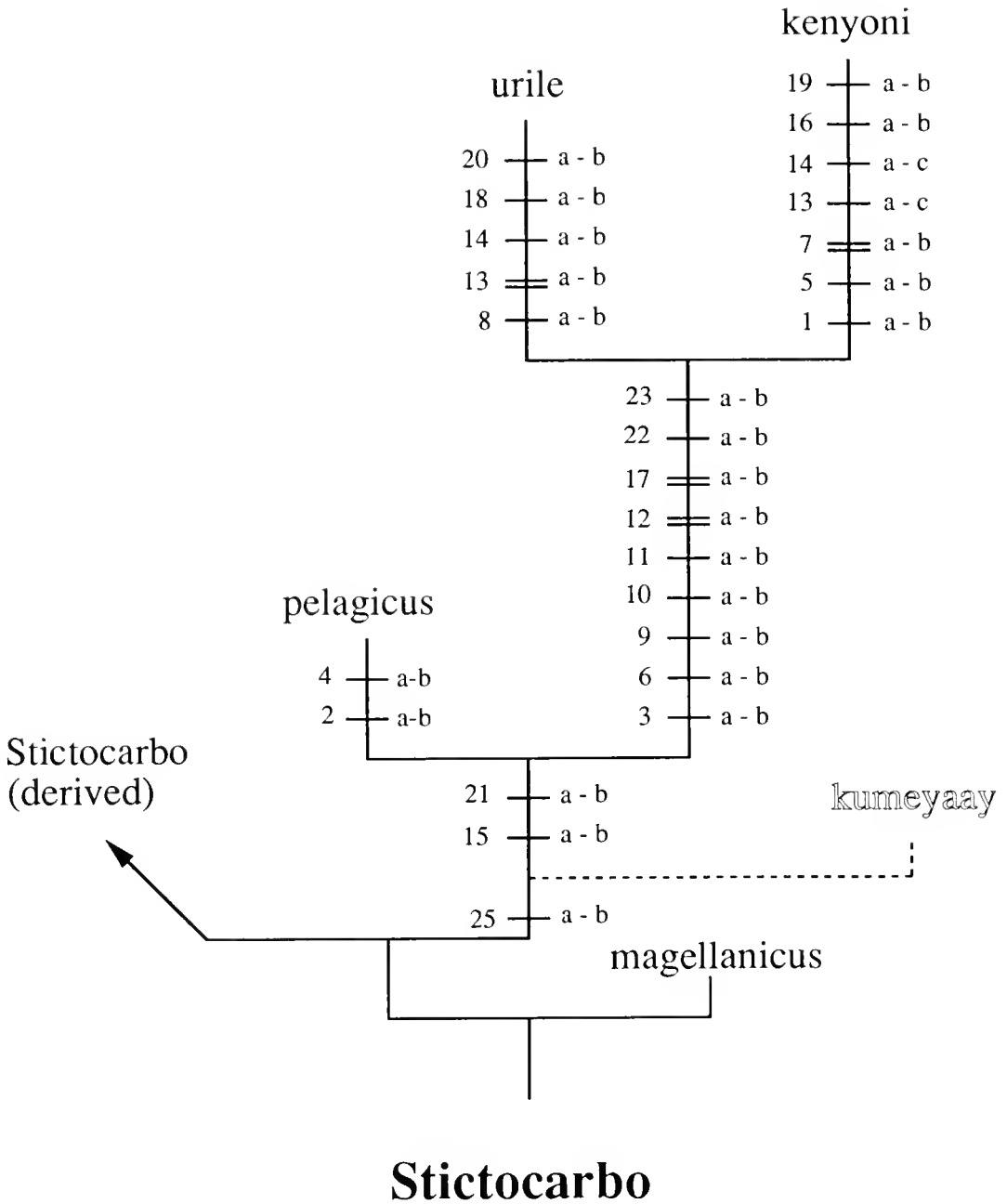


Fig. 3. Tree of the character changes for North Pacific Shags. Solid lines represent derived characters and parallel lines are characters convergent elsewhere in the family (not shown). The number to the left of the character state symbol is the character number described in Appendix 1; the letter sequence to the right is the character state transformation.

of the shaft in *S. kumeyaay* and outgroups, but in *S. pelagicus*, *S. urile*, and *S. kenyoni*, they are wider than the shaft width. The attachment of *M. flexor perforatus digiti III* is on the internal edge of the femoral shaft in *S. kumeyaay*, while in the others it is more medial (see Chandler, 1990, for more extensive discussion). This makes *S. kumeyaay* a sister taxon to present day species of North Pacific shags, but whether or not it is ancestral is problematic.

The union of *S. kumeyaay* and *S. kenyonii* with *S. pelagicus* and *S. urile* implies a more complicated biogeographic history of this clade than was expected before. Previously (Siegel-Causey, 1988), I proposed that Red-faced and Pelagic Shags were descendents of an early branch of Cliff Shags that left the Southern Ocean and moved northward along the west coast of the Americas. The presence of *S. kumeyaay* in the Blancan supports this notion, and may also indicate that shags were recent arrivals to the west coast of North America. All of the other fossil phalacrocoracids known from this region are unambiguously cormorants (Phalacrocoracinae), and date from the early Miocene to the Pleistocene (see Brodkorb, 1963; Olson, 1985). Until earlier shag fossils are discovered, *S. kumeyaay* represents the earliest date for this clade in the North Pacific.

The pattern of relationships among North Pacific shags as shown in my reconstruction of the phylogeny can be used to infer a plausible biogeographic history of the group. The origins of this clade lie in the southern hemisphere; at some time in the Pliocene an ancestral form dispersed from the Southern Ocean into Meso- and North America. Given that most extant shags are associated with cool temperate climates and cold neritic waters, this transequatorial dispersal probably occurred during a major cooling event. Subsequent hypsothermal elevation in temperature and change in oceanographic conditions would have promoted vicariant speciation of the common ancestor of the extant species. After this, it is difficult to speculate on the likely biogeographic sequelae of evolutionary events.

The present-day distribution of extant North Pacific shags suggests that successive vicariance events probably associated with Pliocene and Pleistocene glaciations were the mechanisms for speciation rather than one of dispersal and isolation. Pelagic Shags are amphiberian in the broadest sense and may circumscribe the ancestral distribution of this clade. The greatest abundances of Red-faced Shags lie along the Kurile archipelago and Kamchatkan coast; the Alaskan populations are relatively minor and dispersed (Vyatkin, 1986; Siegel-Causey and Litvinenko, 1992). It is plausible that this species is a Kurilian vicariant with later eastward dispersal into the lower zone of the Bering Sea.

It is noteworthy that all of the misidentified shags were collected from the Pribilof Islands and western Aleutian peninsula. I found a similar pattern of a localized distribution of misidentifications using museum skin specimens (Siegel-Causey, in prep.), which makes it unlikely that the misidentifications were due to chance. The significance of these ambiguous specimens is still unknown.

The biogeographic affinities of Kenyon's Shag are unknown. It is tempting to speculate that this species represents an Okhotskian vicariant originating through isolation in the early Pleistocene. Such a mechanism was proposed for early radiation of *Cephus* alcids into Beringia (Storer, 1952).

It is frustrating that there are few clues to the external appearance of Kenyon's Shag. The fact that there are no previous records of a distinctly plumaged small shag in the North Pacific suggests that Kenyon's Shags are phenotypically very similar to Pelagic Shags. There are many examples of cryptic taxa within species groups in shags; for example, Antarctic and Imperial Shags (*Notocarbo bransfieldensis* and *N. atriceps*; see Siegel-Causey and Lefevre, 1989), and the confusing complex of New Zealand shags (*Nesocarbo campbelli* and *Euleucocarbo* spp.; Voisin, 1973; Siegel-Causey, 1988). Moreover, Pelagic and Red-faced Shags are difficult to discriminate at a distance in field conditions, and sometimes even close at hand (Siegel-Causey, in prep.). Identifications based on locality or size further complicate matters and obscure the nature of distributional patterns.

So far, Kenyon's Shag is known only from Amchitka Island, but I conjecture that more individuals will be found westward, in Okhotskian and Kamchatkan waters. If the collection dates of the types are indicative, then they probably were winter dispersers from less-studied regions to the west. Okhotskian cormorants and shags move east or south in winter (Siegel-Causey and Litvinenko, 1992), and there is historical evidence for other Asian phalacrocoracids in the Aleutians (Siegel-Causey and Lefevre, 1991). Further details of the distribution and ecology of this new species await discovery.

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APPENDIX 1

CHARACTER DESCRIPTIONS

MANDIBLE

1. *Fossa aditus*: (a) extends usually $\frac{1}{3}$ (but no more than $\frac{1}{2}$) the length of the insertion of *M. pseudotemporalis*; (b) extends at least $\frac{3}{4}$ the length of the insertion.
2. *Attachment of M. adductus mandibulae externus superficialis*: (a) absent, reduced, or indistinct; (b) expressed as strong transverse ridge. (Char. 42 of Siegel-Causey, 1988.)

FURCULA

3. *Attachment of M. pectoralis superficialis par superficialis*: (a) the anterior margin is directed posteriorly near the acrocoracoid facet; (b) the anterior margin runs parallel with the anterior edge of the furcula.

HUMERUS

4. *Pneumatic fossa*: (a) lateral surface immediately adjacent to bicipital crest is subplanar; (b) lateral surface marked by distinct, narrow excavation.

5. *Attachment of M. dorsalis scapulae*: (a) proximalmost scar lateral to distal scar; (b) both scars in line on bicipital crest.
6. *Ligamental furrow*: (a) entire length of equal depth; (b) medialmost part marked by deep fossa.
7. *Ligamental furrow*: (a) does not reach head; (b) distinctly notches head. (Char. 64 of Siegel-Causey, 1988.)
8. *Deltoid shaft*: (a) laterodistal surface concave; (b) laterodistal surface strongly convex. (Char. 69 of Siegel-Causey, 1988.)

CARPOMETACARPUS

9. *Infratrochlear fossa*: (a) deeply excavated; (b) indistinct or obsolete.
10. *Carpal trochlea*: (a) area immediately adjacent to supratrochlear fossa broadly and deeply notched into triangular depression; (b) area unexcavated or with a narrow, shallow depression.

SYNSACRUM

11. *Attachment of M. obturator externus*: (a) by distinct fossa; (b) indistinct or obsolete.
12. *Attachment of M. iliacus preacetabulae*: (a) intramuscular line arises on posterior edge of preacetabulum; (b) arises on lateral surface of preacetabulum. (Char. 110 of Siegel-Causey, 1988.)

FEMUR

13. *Attachment of M. obturator externus + internus*: (a) elliptical, shallow, indistinct; (b) deeply excavated, broad, subcircular; (c) deeply excavated, narrow. (Char. 5 of Siegel-Causey and Lefevre, 1989.)
14. *Attachment of M. flexor perforatus digiti II*: (a) indistinct; (b) deeply excavated without noticeable lateral bony margins; (c) deeply excavated with robust lateral bony crest.
15. *Attachment of M. flexor perforatus digiti III*: (a) on internal edge of shaft; (b) on medial edge.
16. *Attachment of M. flexor hallucis longis*: (a) medial margin marked by distinct line just adjacent to medial prominence of external condyle; (b) medial margin coincident with medial prominence, causing the superior aspect to appear sharply produced.
17. *Trochanter*: (a) anterior angle distinct; (b) anterior angle indistinct, curvilinear. (Char. 128 of Siegel-Causey, 1988.)
18. *Intramuscular line between M. flexor perforatus digiti III + IV*: (a) reduced or indistinct; (b) produced into rugose crest. (Char. 120 of Siegel-Causey, 1988.)

TIBIOTARSUS

19. *Supratendinal bridge*: (a) lateral (inferior) width greater than medial (superior); (b) widths equal.
20. *Plantaris fossa*: (a) shallow; (b) excavated. (Char. 131 of Siegel-Causey, 1988.)
21. *Cnemial crests*: (a) robust, close set; (b) thin, widely flared.

TARSOMETATARSUS

22. *Intercotylar fossa*: (a) deeply excavated with strong medial crest; (b) absent or area convex.
23. *Supratrochanteric dorsal fossae*: (a) excavated at digits II, III, and sometimes IV; (b) excavated at digit III only.
24. *Trochlea metatarsus II*: (a) plantar curve simple; (b) strong medioplantar process extends proximally. (Char. 134 of Siegel-Causey, 1988.)

APPENDIX 2

Data matrix of character state codings for North Pacific Shags, genus *Stictocarbo*. Codings for the hypothetical ancestor (not listed) are all primitive. Numbers and codings refer to transformation series and characters described in Appendix 1; codings are: 0 = a, 1 = b, 2 = c, m = missing, U = unordered.

Characters	† <i>kumeyaay</i>	<i>pelagicus</i>	<i>wile</i>	<i>kenyoni</i>
1	m	0	0	1
2	m	1	0	0
3	m	0	1	1
4	0	1	0	0
5	0	0	0	1
6	0	0	1	1
7	0	0	0	1
8	0	0	1	0
9	0	0	1	1
10	0	0	1	0
11	0	0	1	1
12	0	0	1	1
13 [U]	0	0	1	2
14 [U]	0	0	1	2
15	0	1	1	1
16	0	0	0	1
17	0	0	1	1
18	0	0	1	0
19	0	0	0	1
20	0	0	1	0
21	0	1	1	1
22	0	0	1	1
23	0	0	1	1
24	1	1	1	1

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